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The decline of Algerian *Cedrus atlantica* forests is driven by a climate shift towards drier conditions

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ABSTRACT

Some north-African Atlas cedar (*Cedrus atlantica*) forests are in decline, following decades of anthropogenic pressure and repeated drought events. We investigated if the recent decline episodes of these forests are linked to precipitation and temperature shifts, leading to a reduction in tree radial growth and climate-growth un-couplings. Tree-ring width chronologies of Atlas cedar in north-western Algeria allow the identification of climate and growth shifts in these vulnerable Mediterranean forests. Such chronologies, built for six sites, showed common patterns of year-to-year variability during the period 1910-2006. The growth at north-facing sites declined from the 1980s until 2006, whereas the growth at mid-elevation sites declined from the early 20th century until the 1940s, remained stable until the 1980s and then declined until 2006. Cool and wet spring conditions enhanced cedar growth. Sites with fast-growing trees, where growth was strongly reduced by dry summer conditions, showed the most-pronounced negative trends. However, a clear climate-growth uncoupling was observed after the 1970s, when the climate rapidly warmed. We also detected a negative growth shift in the 1980s, when mortality increased. This coincided with changes in early-warning signals of the growth series, such as an increase in the first-order autocorrelation of tree-ring width. All these lines of evidence indicate that the 1980s climate shift towards warmer and drier conditions triggered a shift in cedar growth. The use of radial-growth series as early-warning signals should be further investigated in this species and in other drought-sensitive conifers, given the aridification trends expected for the Mediterranean Basin.

1. Introduction

Several lines of evidence show that a combination of increasing temperatures and droughts (IPCC, 2007) is altering the composition and structure of forests worldwide (Allen et al., 2010; Anderegg et al., 2012). Reduced soil water availability, in conjunction with a rising atmospheric demand for water vapour, is expected to reduce forest productivity, trigger dieback episodes and increase tree mortality (Adams et al., 2017). These warmer and drier conditions are affecting forests across the Mediterranean Basin, where the frequency, intensity and duration of severe droughts have increased during the last 500 years (Cook et al., 2016). For instance, in north-western Africa, the period 1980–2009 is considered as the most-severe drought of the last 900 years (Touchan et al., 2008). This aridification trend is predicted to intensify until the end of the 21st century (Hoerling et al., 2012). Consequently, Mediterranean mountain conifer forests are likely to show growth decline, dieback and mortality in response to warming and drought intensification (Camarero et al., 2015).

In north-western Africa, various conifers have been analysed with regard to their growth–climate relationships, but this region remains understudied in comparison with Southern Europe (but see Touchan et al., 2010, 2017). In this region, the degradation of Atlas cedar (Cedrus atlantica [Endl.] Manetti ex Carrière; hereafter cedar) forests has reached alarming levels, particularly in Algeria. This has led to the local

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disappearance of some cedar populations, which have been replaced by more-drought-tolerant tree species such as *Pinus halepensis* Mill. or *Quercus ilex* L. (Bentouati, 2008; Sarmoum et al., 2018). Cedar is tolerant of drought, but it does not display positive values of net photosynthesis at low water potentials, whereas other Mediterranean species - such as *Q. ilex* - can show net uptake of carbon under such dry conditions (Ladjal et al., 2007). Previous tree-ring studies have confirmed that cedar growth is very sensitive to drought (Esper et al., 2007). In addition, several studies have shown a long-term decline in radial growth in several cedar forests (Kherchouche et al., 2012; Ilmen et al., 2013; Linares et al., 2013; Slimani et al., 2014; Abel-Schaad et al., 2018). Therefore, these forests represent a system that can be used to quantify long-term responses to climate and drought, and to evaluate the post-drought adaptation capacity as well as the existence of refugia.

The current status of Algerian cedar forests indicates that dieback and mortality episodes are linked primarily to unfavourable climatic conditions marked by severe droughts since the 1980s (Kherchouche et al., 2012; Touchan et al., 2017). Therefore, it can be hypothesised that the adaptation capacity of some of these cedar forests has reached a tipping point, leading to irreversible degradation. Here, we test this by assessing if late-20th-century droughts induced an irreversible growth reduction, here regarded as an early-warning signal, which preceded mortality peaks. Thus, we hypothesise that the droughts and warming during the 1980s over north-western Africa negatively affected the growth of cedar forests. We also hypothesise that the recently-detected growth reduction and rise in mortality of some of these forests are related to climate shifts that have enhanced drought severity and uncoupled growth and climate. This study has three specific objectives: (i) to examine whether trends in cedar radial growth varied in response to 20th-century droughts; (ii) to test the temporal stability of climate-growth relationships in relation to the 1980s climate shift, characterised by drier conditions compared with the 1970s; and, finally, (iii) to link the climate-growth uncoupling with the 1980s climate shift.

2. Materials and methods

2.1. Study area and tree species

The cedar is a conifer species endemic to mountainous areas across Morocco (Rif, Atlas) and Algeria (Aurès, Belezma, Hodna, Djbel Babor, Djurdjura, Blida and Ouarsenis) (Benabid, 1994). It occupies a very-fragmented distribution area due to past climatic variations and anthropogenic pressure, leading to the occurrence of scattered forests in different ranges (Cheddadi et al., 2009). This species is better suited to humid and sub-humid climatic conditions and is vulnerable to long and repeated severe droughts, which reduce its rates of photosynthesis (Ladjal et al., 2005, 2007). The cedar stands are dominated by evergreen conifers (cedar, pine and juniper species) but mixed stands with a significant component of evergreen angiosperms (oaks) also abound. These stands range in structure from closed-canopy stands on fertile sites to open-canopy stands (M'hirit and Benzyane, 2006).

The study was conducted in the "Theniet El Had" National Park (TNP), located in the eastern extension of the Ouarsenis massif, north western Algeria (range coordinates 35° 47′ and 35° 54′ N, 01° 54′ and

02° 02′ E) (Fig. A1, Supporting Information). This is a mountainous area occupying 3460 ha, with many steep, north-facing slopes. The altitude varies between 854 and 1786 m a.s.l. The climate is characterised by cool, wet winters (October to March) and hot, dry summers (May to September). The minimum temperature of the coldest month (January) varies between −2.2 and −0.6 °C, and the maximum temperature of the hottest month (July) varies between 27.9 and 32.7 °C. The annual precipitation increases with altitude, from 580 to 868 mm, with only 5% of the precipitation falling between June and August, thus resulting in summer drought. The driest period lasts 3–4 months, from May to September. The snow cover usually lasts 20–30 days, between November and March. There has been a trend towards a drier climate since the 1980s, with a 25% decrease in annual precipitation (Sarmoum et al., 2018). In the study area, the mean annual temperatures have increased since 1950, but annual precipitation has not shown any trend (Fig. A1, Supporting Information). The annual temperatures remained approximately constant until 1940 (mean 15.0 °C), but we have found a subsequent trend towards higher values (ca. + 0.8 °C, mean 15.8 °C), which lasted until 1965. This warmer period was followed by a colder period from 1965 to 1975 (ca. –1.0 °C, mean 14.8 °C). Lastly, the warmest period of the time series analysed was 1980 to 2010 (mean 16.2 °C) (Table A1, Supporting Information). The soils are basic and shallow, and formed on sandstones and marls.

In the TNP, *C. atlantica* forests occur between 1200 and 1786 m a.s.l. but are scarce below 1300 m. The stands included in the study area are dominated by *C. atlantica*, often mixed with *Quercus ilex* L. subsp. *ballota* (Desf.) Samp and *Quercus faginea* Lam., and, to a lesser extent, *Pinus halepensis* Mill., *Quercus suber* L. and *Juniperus oxycedrus* L. The region has regularly suffered dieback episodes during the last few decades (Kherchouche et al., 2012).

2.2. Tree sampling and radial growth data

Sampling was conducted during January 2007. Six 60 × 50 m plots were established in *C. atlantica* stands, according to a stratified random design, by selecting sites with different topographic conditions (elevation, exposure, slope) and vegetative composition (Fig. A1; Table 1). In total, 90 dominant trees were sampled, and we measured diameter at breast height (1.3 m above ground level –dbh- cm) and height (H, m), using a caliper (Haglöf Mantax, Sweden) and a Vertex III hypsometer (Haglöf Sweden) (Table 1), respectively. We selected the 15 largest (dominant) cedar individuals. Two cores per tree at breast height were taken using a 5-mm Suunto® increment borer, in a direction perpendicular to the steepest slope. The cores were mounted, sanded and polished, and visual cross-dating was performed under a binocular microscope, following standard dendrochronological methods (Speer, 2010). The tree-ring widths were measured to the nearest 0.01 mm using a LINTAB measuring device and the Time Series Analysis Program (TSAP). The visual cross-dating was later verified using COFECHA software (Grissino-Mayer, 2001). To estimate the recent mortality rate of cedars in the study sites, we calculated the frequency of trees forming the last ring after 1972 and until 2005 in both cores, which we assumed corresponded to recent dates of death.

We standardised and detrended the tree-ring width (TRW) data

Table 1

Site description, geographic coordinates, elevation, aspect, slope, soil and tree and stand features of the sampled *Cedrus atlantica* trees in the "Theniet El Had" National Park (northwest Algeria). Mean values ± standard errors are shown.

Site	Latitude (N)	Longitude (E)	Elevation (m a.s.l.)	Exposure	Slope (%)	Forest type	Diameter at 1.3 m (cm)	Height (m)
Djoua	35° 52' 24'	1° 58' 25''	1420	NNW	30-40	*C. atlantica*	41.2 ± 3.6	17.5 ± 1.1
Guar	35° 52' 06''	1° 58' 01''	1325	NE	10-20	*C. atlantica, Quercus ilex, Pinus halepensis*	32.8 ± 2.0	15.8 ± 0.9
Ouar	35° 51' 50''	1° 57' 27''	1550	SW	50-60	*C. atlantica, Quercus faginea, Quercus suber*	22.8 ± 1.8	11,6.0 ± 0.4
Pep	35° 53' 23''	2° 00' 02''	1460	NNE	20-30	*C. atlantica*	45.8 ± 3.5	17.6 ± 0.9
Tour	35° 51' 44''	1° 59' 18''	1520	NNE	50-60	*C. atlantica*	52.1 ± 2.5	18.2 ± 0.6
Ain	35° 53' 34''	1° 39' 25''	1300	NW	20-50	*C. atlantica, Quercus ilex, Pinus halepensis*	29.8 ± 2.5	13.7 ± 1.0

using common dendrochronological procedures. We fitted negative exponential functions to the raw ring-width data and obtained indices by the performance of autoregressive modelling of the standardised index series, to remove temporal autocorrelation and to generate residual ring-width indices (RWIs). Finally, a biweight robust mean was used to compute the mean residual chronologies of the RWIs for each stand. In total, six residual site chronologies were created.

The tree-ring width data were characterised using the following statistics: mean ring width, first-order autocorrelation of raw tree-ring widths (AC1), mean sensitivity (MS) and mean correlation between individual series of RWIs (Rbar). To assess how well replicated each chronology was, the Expressed Population Signal (EPS) was calculated, since EPS values > 0.85 indicate sufficient agreement and replication for dendroclimatic analysis (Wigley et al. 1984). The dplR library (Bunn et al., 2018) was used to calculate the dendrochronological statistics.

2.3. Climatic data

The availability of homogenous and long-term climatic data from weather stations located close to the study sites is very limited. Therefore, we used 0.5˚-gridded monthly data for the mean temperature and total precipitation, available for the period 1901–2006 from the Climate Research Unit (CRU) version 3.24 (CRU, 2008; Harris et al., 2014). These data were downloaded using the Climate Explorer webpage (https://climexp.knmi.nl/) and were used to quantify trends in annual climatic variables and to assess the climate-growth relationships. We also obtained monthly gridded (0.5˚ resolution) data of drought severity using the Self-calibrating Palmer Drought Severity Index (scPDSI) for the period 1901–2006 (van der Schrier et al., 2013). The scPDSI was also used to select the four most-intense droughts in the study area for the period 1975–2016.

2.4. Climate–growth relationships

We calculated Pearson correlations and response functions to correct for the interdependency among climatic variables, using residual chronologies as response variables and monthly climatic variables (mean maximum and minimum temperatures, precipitation) and the scPDSI as predictors. We used the Treeclim package to calculate correlation and response coefficients (Zang and Biondi, 2015). The window of the analyses was from October of the previous year until September of the current year (i.e. the year of tree-ring formation). Correlations were calculated for the common period 1910–2006. The significance of the correlations was estimated through bootstrapping. Moving correlations were calculated for each site by selecting the significant response coefficients. We calculated these moving correlations considering 20-year-long intervals shifted by one year for the period 1901-2006.

2.5. Spatiotemporal patterns and trends in radial growth

To quantify trends in radial growth in different cedar populations, we applied a linear mixed-effects models (Pinheiro and Bates, 2001) of the type:

$$Y_i = X_i\beta + Z_ib_i + \varepsilon_i \qquad (1)$$

where Y_i is the response variable (TRW), β is the vector of fixed effects (site, year, tree age, tree *dbh*, site: year interaction), b_i is the vector of random effects (tree identity), X_i and Z_i are, respectively, fixed- and random-effects regressor matrices and ε_i is the error vector. In the models, site is a factor representing the different populations and calendar year is a variable that accounts for changing TRW trends through time. Tree age and *dbh* were included in the models to allow for potential differences in growth trajectories among trees of differing age and size. We included an interaction between site and calendar year to

account for potential differences in the growth trends between populations. Tree identity was included as a random factor to account for the fact that each tree sample represents repeated measurements from the same individual. The trees were nested within each site when included in the model. We included in the models a first-order autocorrelation structure (AR1) to account for the dependency of the growth in year t on the growth in the previous year t-1. The TRW was log-transformed (log TRW + 1) prior to the analyses to achieve normality. The model residuals followed a normal distribution. To quantify the strength of the model, we calculated a pseudo–R^2 (Nakagawa and Schielzeth, 2013). Lastly, a graphical examination of the residuals and fitted values was carried out to detect the influence of outliers and to evaluate the general model fit.

To evaluate the potential shared variance in the RWIs series, which reflects the common growth variability, a principal component analysis (PCA) was conducted on the covariance matrix of all the cedar RWIs chronologies. A rotated Varimax PCA was calculated for the 1910–2006 period. We performed all multivariate analyses using the *vegan* package in R (Oksanen et al., 2013).

A multi-model inference approach based on information theory was applied to identify the set of covariates that best explained tree growth trends (Burnham and Anderson, 2002). We ranked all the potential models according to the second-order Akaike information criterion (AICc) (Aho et al., 2014). We also calculated the Akaike weight of the selected model (w_i), which is the relative probability that quantifies whether the selected model is the best one.

When significant interactions were found between the calendar year and site, we performed least-squares means analysis based on Tukey HSD tests to assess the differences between populations (Bretz et al., 2010). In order to account for the fact that growth trajectories may change across time, two separate analyses were performed. First, we studied the TRW trends for the most-replicated period (1953–2006). Second, we studied the growth trends from the year 1970 onwards (1971–2006).

2.6. Detection of shifts in climate and growth data

We identified shifts in the summer climate data (mean temperature, precipitation) (cf. Esper et al., 2007) and also in the site mean series of RWIs, considering the 1950–2006 and 1900–2006 periods, respectively. We used a robust and simple regime-shift detection technique to calculate shifts in mean values (Rodionov, 2004,2006). In short, this method is based on an algorithm that calculates cumulative deviations from the mean and obtains a Regime Shift Index (RSI), which is a cumulative sum of the normalised anomalies (Rodionov, 2004). The RSI allows the magnitude and duration of the abrupt changes in a variable to be monitored through time (i.e. shifts). Since the two periods analysed differed, we considered cut-off segment lengths of 10 and 20 years for the climate and ring-width data, respectively. In both cases, we calculated an RSI (the sum of the normalised anomalies with respect to the mean) and considered regime shifts to be significant (i.e. the existence of an actual shift) at $p < 0.05$. We also calculated trends in monthly climate data (temperature, precipitation) and the scPDSI using the Kendall tau coefficient (Kendall, 1938).

We also explored the presence of early-warning signals in the growth data of *C. atlantica* trees at each sampled site. We used several statistical techniques to evaluate whether critical transitions could be detected in a growth series. A critical transition to a new state (tipping point) is preceded by early-warning signals reflected in time series statistics (Dakos et al., 2012a). In particular, the first-order autocorrelation (AC1) or the standard deviation (SD) of a time series varies near a tipping point (Dakos et al., 2012b). Here, we quantified the AC1 of the residuals of the mean ring-width series, which were previously detrended by applying a Gaussian filter that was 22% of the time studied (i.e., 20 years). These residuals of ring-width were then analysed using 20-year-long moving windows, but without pre-whitening in
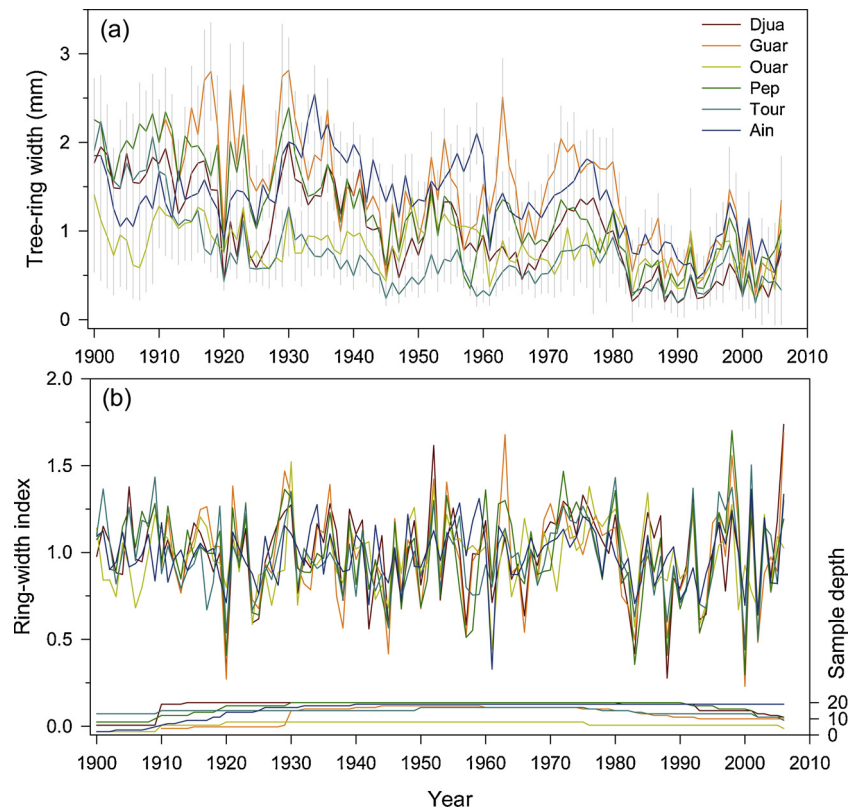
Fig. 1. Variation in tree-ring width (a) and ring-width indices (b, residual chronologies) of *Cedrus atlantica* site chronologies for the 1900–2006 period. Sample depth is shown as lines (right-y axis in the lowermost plot.).

order to be able to assess the changes in short-term growth persistence. We expected an increase in AC1 and SD near the tipping point. These analyses were carried out using the *early warnings* package (Dakos et al., 2012a). All analyses were carried out using the R statistical package version R-3.5.2 (R Development Core Team, 2016).

3. Results

3.1. Spatiotemporal trends in climate and radial growth

We identified different temporal trends in the radial growth of *C. atlantica* trees in the forests of north-western Algeria over most of the 20th century (Figs. 1 and 2). We provide further evidence that these temporal changes also reflect non-stationarity in the climate-growth relationships of *C. atlantica* over the 20th century, which also differed among sites (Figs. 3 and 4). These changes corresponded to growth shifts triggered by drier conditions (Fig. 5).

Synchronous growth reductions were detected in 1919, 1945, 1965, 1983, 1988 and 2000, corresponding to droughts. In the first half of the 20th century the frequency of wide rings was much higher than in the second half, suggesting a shift toward more-arid conditions (Fig. 1). Indeed, at the location Tour there was a marked reduction in growth variability from the mid-1920s onwards, and in all populations the growth variability tended to decline after the 1980s. All tree-ring width series displayed significant first-order autocorrelation, and some populations (Djoua, Pep, Tour and Ain) showed higher values of this variable and a relatively-higher common growth variance among trees (Table 2). The mean sensitivity differed among populations.

Growth (TRW) was mainly determined by changes through time, but it was also affected by changes in tree size (*dbh*) and age, and by site conditions. The model for the entire study period (1953–2006) accounted for 48% (pseudo-R^2) of the variation in growth (TRW); 41% and 27% of the variance corresponded to fixed and random factors,
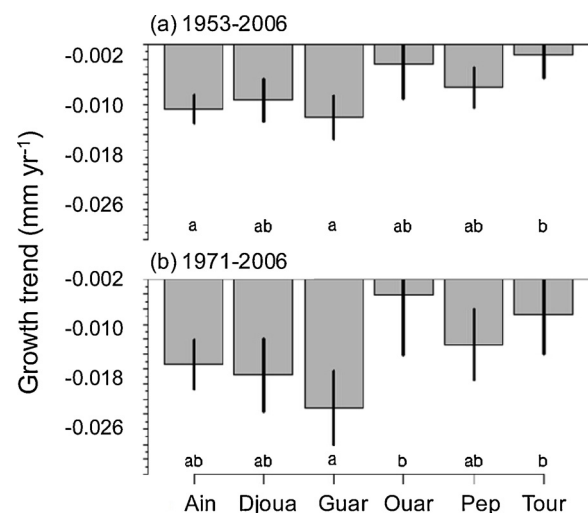

Fig. 2. Growth (tree-ring width) trends (slope coefficients(estimated for the periods 1953–2006 (a) and 1971–2006 (b) in the six *Cedrus atlantica* sites. Bars show mean trends with their standard deviation (error bars). Different letters indicate significantly ($p < 0.05$) different trends between sites according to Tukey HSD tests.

respectively. The w_i of this model was 98%, and it included the following variables: tree *dbh* ($F = 66.5$, $p < 0.01$); site ($F = 17.16$, $p < 0.01$); calendar year ($F = 151.32$, $p < 0.01$); tree age ($F = 10.34$, $p < 0.01$); and the interaction between site and calendar year ($F = 4.67$, $p < 0.01$; Table 3). The model for the period 1971–2006 accounted for 47% of the variation in TRW (39% and 22% being due to the fixed and random factors, respectively). The w_i of this model was 89%, and it included the following variables: tree *dbh* ($F = 44.8$, $p < 0.01$); site ($F = 9.82$, $p < 0.01$); calendar year ($F = 123.4$, $p < 0.01$);
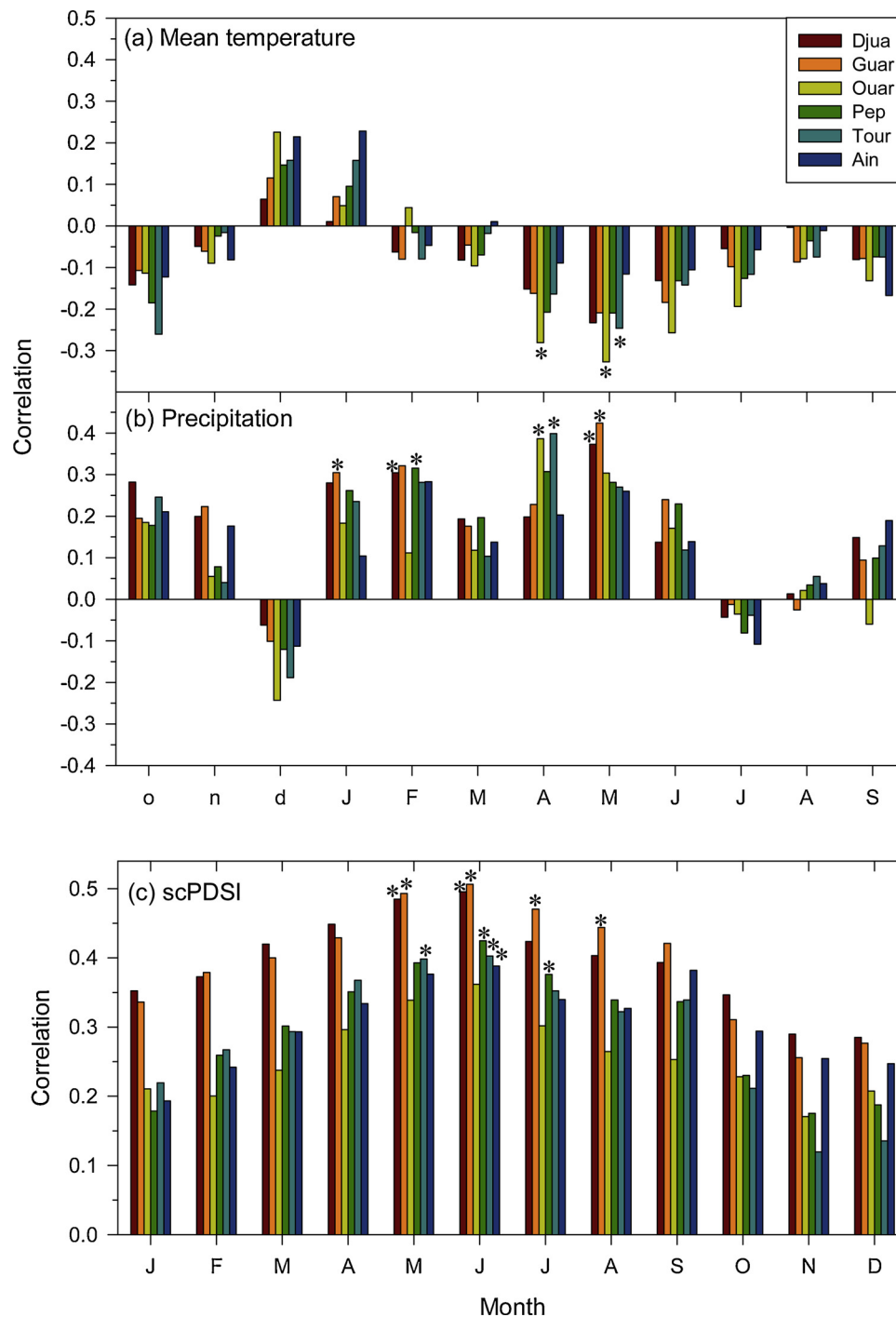
Fig. 3. Pearson correlation coefficients obtained by relating ring-width indices (residual chronologies) and monthly climatic data (a) mean temperature; (b) precipitation, and (c) drought scPDSI index for *Cedrus atlantica* populations. Monthly climatic variables from the previous and current years are abbreviated by lower- and upper-case letters, respectively. Asterisks indicate significant ($p < 0.05$) response coefficients. Correlations were calculated for the common period 1910–2006.

tree age ($F = 7.37$, $p < 0.01$); and the interaction between site and calendar year ($F = 3.44$, $p < 0.01$).

The estimated TRW trends showed differences among sites during the two considered study periods (Fig. 2). Site Guar showed the most negative trends, followed by Ain and Djoua, while Ouar and Tour had the least-negative trends. Sites with fast-growing trees showed negative trends (Fig. 1, Table 2).

The first (PC1) and second (PC2) components of a PCA accounted for 74.3% and 8.2%, respectively, of the variance in the *C. atlantica* residual chronologies (Fig. A2; Supporting Information). All chronologies shared similar loadings in the PCA biplot, except those of Ouar

and Ain - which showed the lowest PC1 scores. In fact, all the residual chronologies were significantly ($P < 0.001$) correlated among themselves for the common period 1910–2006, but the correlations varied greatly, with the pairs Djoua-Guar and Ain-Ouar being the most ($r = 0.82$) and least ($r = 0.46$) correlated, respectively. The mean correlation suggests two common patterns of variability in growth: sites Djoua, Pep, Tour and Guar vs. Ouar and Ain (Fig. A2). These two groups correspond, respectively, to populations with some water compensation for high-elevation and/or north-facing pure cedar stands (e.g. Djoua) and to populations in drier locations for high-elevation and south-facing pure cedar stands (e.g. Ouar) or low-elevation sites (e.g. Ain).
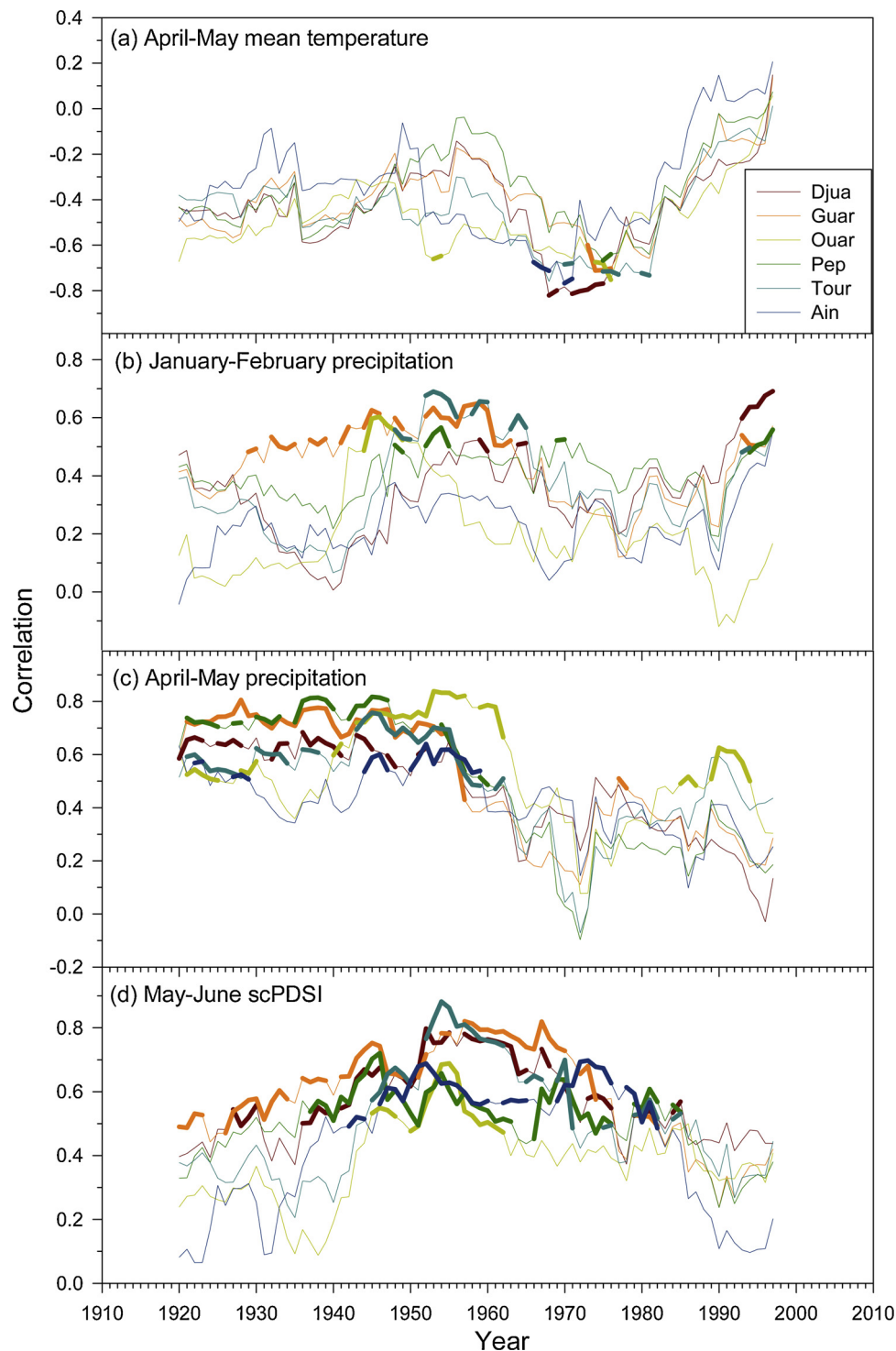
Fig. 4. Moving correlations calculated between residual chronologies (ring-width indices) of *Cedrus atlantica* and main climate variables: (a) April-May temperature, (b) January-February precipitation, (c) April-May precipitation, and (d) May-June scPDSI index. Correlations were calculated considering 20-year intervals for the 1901–2006 period. Continuous, thick lines indicate significant correlations ($p < 0.05$).

Populations of *C. atlantica* located at north-facing exposures experienced growth increases starting in the 1900s and again in the 1930s, and later plateaued in the 1950 s–1970 s. The growth of these populations declined until the early 21st century. In contrast, growth in the mid-elevation stands declined significantly and steadily from the beginning of the 20th century, but afterwards remained relatively similar to that of the north-facing populations until the 1940s. The radial growth in these populations remained stable until the 1980s and declined afterwards.

3.2. Climate-growth associations and responses to drought severity

With respect to the influence of the climate of the previous year on growth, growth at Tour displayed significant negative correlations with the October temperature, whilst at Ain growth was positively correlated with the December temperatures. At sites Djua, Tour and Ain there was a positive correlation between growth and the prior autumn precipitation. Higher spring temperatures were negatively correlated with growth (Fig. 3a), and some stands also showed negative associations
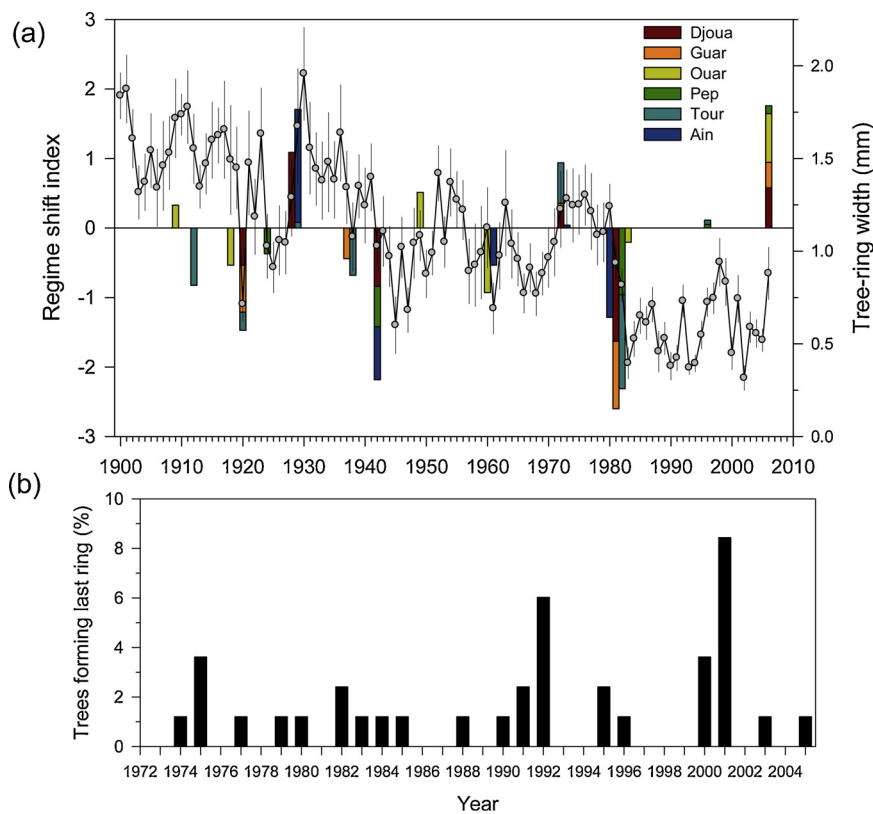
Fig. 5. (a) Regime shifts of *Cedrus atlantica* growth (calculated on mean site series of ring-width data) observed in the study area after 1900 and mean regional ring-width series (line with symbols; values are means ± SE). In the plot (a) the bars show the positive or negative regime shift index values. (b) Frequency of trees forming the last ring after 1972 and until 2005 corresponding to recent death dates.

Table 2

Dendrochronological statistics of the six *Cedrus atlantica* study sites. The statistics were calculated for the period 1910–2006 when the sample depth (number of measured trees) reached maximum values. Variables' abbreviations: AC1, first-order autocorrelation of tree-ring width; MS, mean sensitivity (MS) of residual ring-width indices; Rbar, mean correlation among series; EPS, Expressed Population Signal.

Site	No. trees (No. cores)	Age (year ± SD)	Mean tree ring width ± SD (mm)	AC1	MS	Rbar	EPS
Djoua	15 (25)	121 ± 16	1.08 ± 0.68	0.80	0.29	0.51	0.94
Guar	15 (30)	89 ± 11	1.48 ± 0.89	0.64	0.35	0.48	0.95
Ouar	15 (23)	96 ± 8	0.96 ± 0.42	0.63	0.37	0.48	0.97
Pep	15 (29)	110 ± 16	1.27 ± 0.82	0.79	0.43	0.47	0.94
Tour	15 (28)	130 ± 18	0.91 ± 0.67	0.82	0.38	0.51	0.94
Ain	15 (30)	92 ± 10	1.36 ± 0.74	0.76	0.25	0.39	0.87

with autumn temperatures. At sites Djua, Guar, Ouar, Pep and Tour, the RWIs were negatively correlated with the May temperature, while only Ouar showed a negative correlation with the April-June temperatures. Winter and spring rainfall (except that of March) usually showed a positive correlation with growth at all sites. The highest correlations were found with the early spring precipitation (April and May). Throughout the 20th century the growth response to precipitation was mainly positive (Fig. 3b). Cedar growth was related positively to the scPDSI from April to September of the current year (Fig. 3c). Maximum growth-scPDSI correlations were observed in June, at the 14-month scale and for the Djoua and Guar sites. The response functions emphasised the positive effects of wet and cool April-May conditions on growth and the detrimental effects of cumulative drought stress from May to July. Finally, the spatial correlation of the PC1 scores (resulting from the PCA of the RWIs) with the scPDSI June drought index (Fig. A3, Supporting Information) evidences the climate sensitivity of the Algerian cedar populations. This analysis revealed that dry conditions in June were associated with reduced cedar growth across the study

Table 3

Summary statistics (estimated coefficients) of the three most parsimonious linear mixed models fitted to radial growth data (tree-ring width) of cedar populations as a function of tree size (*dbh*, diameter at breast height), site, calendar year, tree age and the interaction between site and year. Models were fitted to TRW data of the best-replicated period (1953–2006) and the 1971–2006 period. AICc and w_i are the second-order Akaike information criterion and the Akaike weight (relative likelihood of the model), respectively. The symbol "+" indicates that the selected variable was entered into the model. Significance levels of fixed effects: *$p <$ 0.05, **$p <$ 0.01, ***$p <$ 0.001.

Intercept	*dbh*	Site	Year	Age	Site : year	log-likelihood	AICc	w_i
Period 1953-2006								
17.50**	0.0022*	+*	− 0.0086**	− 0.0029*	+**	1053.79	− 2073.4	0.98
17.26**	0.0021*	+*	− 0.0086**		+**	1048.81	− 2065.5	0.02
13.91**	0.0022*	+*	− 0.0068**	− 0.0027*		1042.51	− 2060.9	0.01
Period 1971-2006								
23.06***	0.0021*	+*	− 0.0114***	− 0.0028*	+***	743.54	− 1452.8	0.89
22.85***	0.0020*	+*	− 0.0114***		+***	740.04	− 1447.8	0.09
21.40**	0.0020*	+*	− 0.0106***	− 0.0026*		735.17	− 1446.2	0.03

region in northern Algeria.

From 1920–1990, the growth and April-May temperatures were negatively correlated (Fig. 4a). The correlation coefficients between growth and the April-May precipitation were highest and significant in the early 1920s, but a sharp change to non-significant correlations occurred in the 1960s (Fig. 4c). Similar responses were found for the May-June scPDSI (Fig. 4d). This decrease in correlation coincided with the emergence of significant positive correlations with the January-February precipitation and a clear shift of the correlations with the April-May mean temperature towards positive values.

3.2.1. Regime shifts of growth

The regime shift index (RSI) of cedar growth showed positive and negative values throughout the 20th century (Fig. 5a). However, we detected a climate shift corresponding to 1941, for almost all the cedar sites, followed by a negative shift in 1980-1982. These two shifts were consistent with those observed for temperature and precipitation (see also Fig. A1). However, the timings of the shifts differed among sites. It is noteworthy that these 1980s growth shifts preceded the increase in cedar mortality during the late 20th century (Fig. 5b). Lastly, positive RSI values were observed in 2006, which reflect a certain degree of growth recovery.

The early-warning indicators (AC1, SD and r) in the cedar growth series shifted after the first half of the 20th century (1930–1970), when the AC1 values were below 0.6, the values becoming higher and more variable during the latter part of the century after 1970, before diminishing during the final part of the 20th century (Fig. 6). The SD and *r* values also started to increase after the 1970s growth shift.

4. Discussion

We wished to quantify growth trends in Algerian cedar forests in response to the climate in the 20th-century and assess if climate-growth relationships were stable during this period. We found growth shifts related to the 1980s climate shift, which was characterised by a sharp change towards hotter and more-arid conditions in north-western Algeria. These shifts explained the instability in climate-growth relationships throughout the 20th century. Furthermore, the 1980s climate shift preceded an increase in cedar mortality, which suggests that: (i) hotter droughts induced dieback in some of the forests studied, and (ii) the increase in tree mortality was related to this aridification trend.

The climate-growth relationships were relatively similar among the populations during the first half of the 20th century but they altered (i.e. for spring precipitation and temperature) after the 1970s, when warming intensified across the western Mediterranean Basin (Figs. 3 and 4). This climate shift towards warmer and drier conditions in the 1980s coincided with several signals of impending cedar decline and vigour loss (Figs. 2, 5 and 6): a long-term decline in growth, negative growth shifts, changes in early-warning indicators of growth (such as AC1, SD and *r*) and an increase in cedar mortality.

Relationships between the tree-ring width and climate are assumed to be stable over time, but climatic shifts may make these associations unstable, changing the sensitivity of tree growth to climate (Camarero et al., 2018). However, very few studies so far have analysed growth shifts that are potentially climate-related by focusing on a particular species, such as cedar, showing recent increases in mortality (Kherchouche et al., 2012). This study evidences that climate-growth relationships are unstable through time. In addition, our findings allow such climate-growth uncoupling (see Fig. 4) to be linked with growth decline (cf. Figs. 2 and 5) and increased mortality in Algerian cedar forests.

4.1. Spatiotemporal trends in radial growth during the 1910–2006 period

We found a long-term and positive association between growth and spring precipitation and the opposite relationships for spring

temperature and drought severity among *C. atlantica* populations in north-western Algeria (Fig. 3). These responses are similar to those reported in the literature for cedar forests and other Mediterranean tree species, which usually show a negative response to drought stress (i.e. warm and dry conditions) during the early part of the growing season (Kherchouche et al., 2012; Slimani et al., 2014). These responses are probably linked to the sharp drop in mesophyll photosynthesis rates caused by warm conditions and increased vapour pressure deficit (Ladjal et al., 2007). However, growth was also affected by tree size and age, suggesting that the drought sensitivity of cedar depends on tree size and age (see Linares et al., 2013), two variables which affect the hydraulic efficiency of trees.

However, our results reveal that while growth was sensitive to drought over the entire study period, the dependence of growth on spring precipitation (e.g. April-May) relaxed after the mid-20th century (Fig. 4c). This phenomenon occurred in parallel with a decrease in the sensitivity of growth to the spring temperature and the scPDSI (Fig. 4a and d). Consistent with our findings, non-stationary climate-growth relationships have also been found in other conifers across the Mediterranean Basin in the 1950s and 1970s (Lévesque et al., 2014). A likely reason for the increase in the sensitivity of tree growth to temperature is the shift towards warmer and drier spring conditions after the 1970s (Camarero, 2011). Additionally, processes associated with changes in the growing season and snow dynamics (snowfall and snowmelt) may produce changes in moisture availability, with a stronger negative impact of a decrease in spring precipitation on tree growth (e.g., a shortening of the growing season through lack of snow or rapid snowmelt) (Xu et al., 2016). Non-stationary responses of radial growth to climate may reflect changes in site conditions along altitudinal gradients, as the PCA indicated and as has been found in other mountainous areas (Trujillo et al., 2009). Higher water availability due to a deeper snowpack at higher elevation may extend the growing season and, ultimately, affect the water balance of populations located at high-altitude sites. Furthermore, dendrochronological studies have shown that tree age does not have major effects on cedar growth responses to inter-annual climatic variability (Linares et al., 2013).

4.2. Uncoupling of growth and climate after the 1970s in Algerian cedar forests

The growth of cedar has undergone different shifts over the past *ca.* 100 years and, consequently, the relationship between growth and climate is unstable (Fig. 4). Our results confirm that *C. atlantica* growth became uncoupled from precipitation after the 1970s shift, coincident with a change in climatic conditions in this region. These climate shifts may have a substantial impact on the growth and vitality of Algerian cedar forests, because this is the easternmost limit of the distribution of this species – where the climate is warmer and drier than in the western part. Analogous to our findings, previous dendroclimatic research on other conifer forests has found uncoupling of climate–growth associations, mainly caused by continued and rapid warming trends and drier conditions (Girardin et al., 2016; Camarero et al., 2015, 2018), indicating that these climate shifts affect several components of forest dynamics, such as growth and, possibly, mortality and regeneration (Sarmoum et al., 2018).

The post-1970s climate shift led to climate-growth uncoupling in Algerian cedar populations as a result of drier and warmer conditions, which probably increased the atmospheric water demand, leading to higher vapour pressure deficits and decreasing carbon uptake and growth (Aussenac and Finkelstein, 1983). After the 1970s, climate shifts leading to drier conditions caused negative growth across Mediterranean conifer forests (Touchan et al., 2017). Related to these climate and growth shifts, severe tree mortality and widespread crown dieback episodes have been observed in other Mediterranean conifer forests (Camarero et al., 2015).

However, there are other factors that may be involved in the
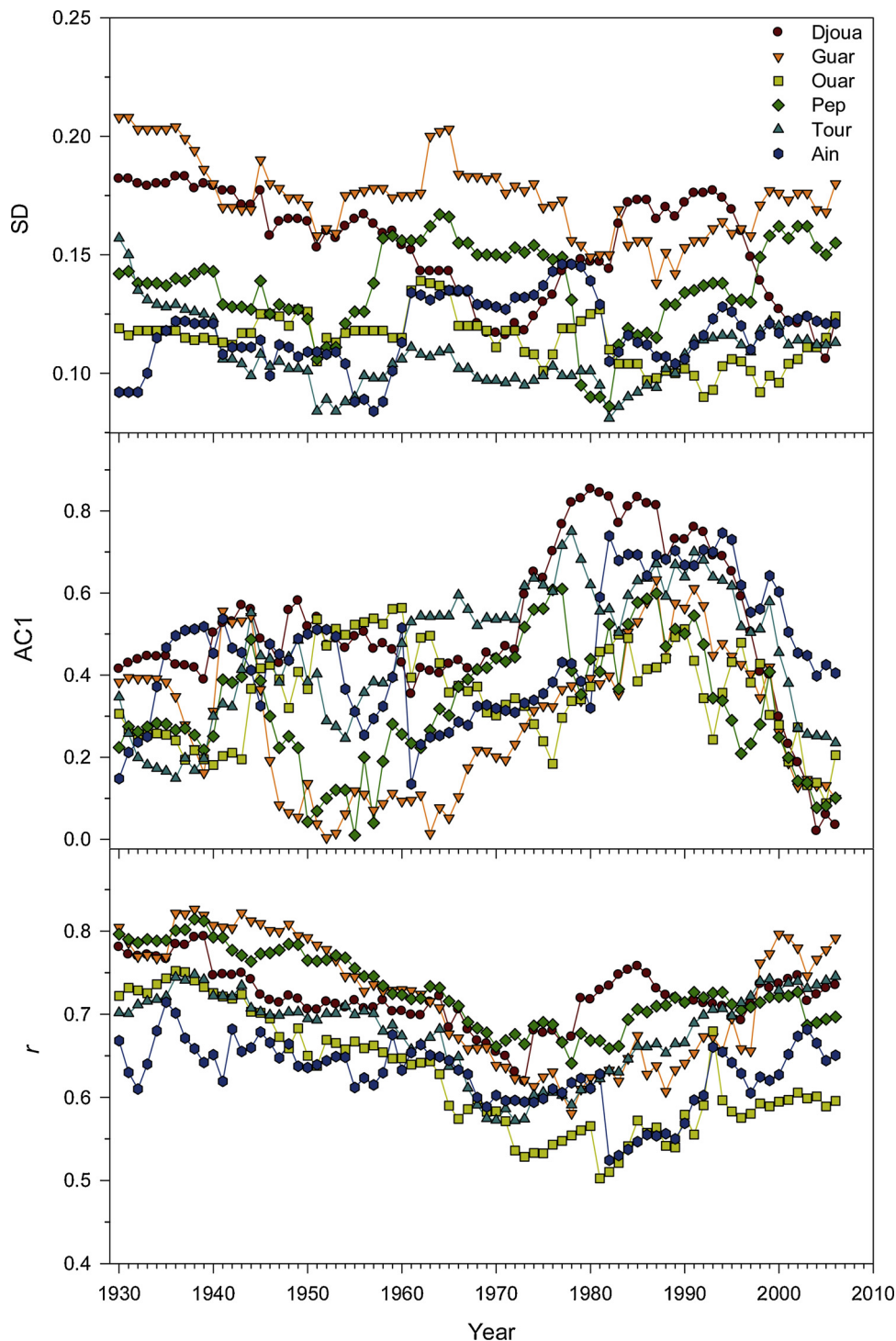
Fig. 6. Summary of early-warning warning statistics applied to indexed ring-width series of *Cedrus atlantica*. The figure shows the standard deviation (SD), the first-order autocorrelation (AC1), and the mean correlation between each tree ring-width series and the site mean series (*r*). In all cases, statistics were calculated for 20–year long windows from 1910 to 2006. In the plots the year indicates the last year of each 20-year interval (e.g., 1930 corresponds to the 1910–1930 interval).

uncoupling of climate and growth: heterogeneity in the climatic data sources, the influences of additional factors on these ecosystems, the role of refugia as sites where genetic diversity may affect growth sensitivity, or site-specific climatic conditions related to topography or soils (see Cheddadi et al., 2017). The choice of the climate dataset, with the precipitation data being of particular concern, affects the capacity to identify climatic trends, especially during the first half of the 20th century (Wu et al., 2017). This is important at sites where the quality of the climatic data is low, as in mountainous areas of northern Africa

(Wilson et al., 2007). Additionally, other drivers or stress factors, such as changes in management and use (e.g., traditional logging), which are recurrent in Circum-Mediterranean cedar forests (Bassil et al., 2018), could have affected the data by disrupting the growth responses to climate, thereby causing the uncoupling. Nevertheless, we did not observe any obvious abrupt decline in growth, typical of severe defoliation due to insect infestations (Sangüesa-Barreda et al., 2014), and there are no reports of such events or changes in forest use in the studied stands, at least in the second half of the 20th century. Therefore,

changes in climate seem the most-plausible drivers of the uncoupling.

5. Conclusion

Our findings represent a new contribution to the examination of radial growth patterns and responses to climate across the cedar distribution in north-western Africa. Climate-growth relationships were unstable in this species and a negative growth shift was triggered by a climate shift towards drier conditions in the 1980s. This climate shift led to growth decline and coincided with high cedar mortality at the turn of the 20th century. Tree-ring data may serve as early-warning indicators of impending mortality, as we have shown in the case of cedar forests. Climate predictions for these forest ecosystems indicate continued and rapid warming and increased aridification in the 21st century, which would threaten some Atlas cedar forests. More-arid conditions would raise Atlas cedar mortality rates and trigger compositional shifts towards forests dominated by species better able to tolerate drought, such as *Q. ilex*. Therefore, long-term efforts will be required to monitor the impacts of climate warming and to develop mitigation solutions, in particular through integration of national forest inventories and dendrochronological data. This will help to provide large-scale systematic and coherent information on the post-drought adaptation capacity of Atlas cedar forests. Structural and tree-ring data could aid the identification of vulnerable forests and stands, where mitigation measures (e.g., thinning) should be applied to alleviate the negative impacts of the forecasted hotter droughts.

Acknowledgments

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.dendro.2019.04.003.

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